Present problems in the anatomy, morphology, and biology of the Cactaceæ.

W. F. GANONG.

[*Concluded from p. 138.*]

The development of the flower is unknown, excepting for references by Goebel and others. It is likely to prove of great interest, and may throw light upon the relationships of the family, as it certainly will of the genera. Biologically it is equally unknown, Schumann, Goebel and Loew giving it but the barest reference. How is it fertilized? How generally are the stamens sensitive or the flowers dichogamous? Why sometimes so evanescent? Why are the flowers often so showy? Do they illustrate the principle of showiness in proportion to scarcity of insects? Do the colors contrast with the background simply, or do they attract particular groups of insects? How do the less showy Mamillarias thrive? Is self-fertilization common? By what animals is the dissemination of the fruit effected? How are the dry fruits of Echinocactus and some Opuntias scattered? In berries, what is the meaning of the white and red colors; do they simply contrast with the background, or do they attract specific animals? How are bristle-covered Opuntia berries eaten? Are they picked at by the bills of birds and neglected by mammals? The pulp has been found in several species to be formed chiefly by the funiculus of the seed, though the wall of the hollowed receptacle co-operates. The extremely "inferior" character of the ovary of Cactaceæ leads us to question whether there be a biological reason for it. If so, is it to be found in protection to the ripening ovary, or in utilization of the receptacle to help form an edible berry? In some species, as Goebel has shown, the seeds germinate in the fruit. What does this mean? How are such fruits scattered? Upon the surface of some fruits, new branches appear; do they occur when those fruits have seeds?

Species of Cereus often show a sudden crest, forming where the few ribs are replaced by very many. What conditions determine this? How does the vegetative point act in the transition? The stems of several genera often show a close crowding together of the spine-clusters, suggesting that the stems shorten as roots sometimes do in the ground. Do they shorten, or is the crowding simply the result of the pressing together of the spine clusters as the curved ribs straighten out in growth? It is easy to see an advantage for the shortening, as it would allow of a considerable development of new green tissue each year without an equivalent lengthening of the entire stem, and condensation is always an advantage to them. Moreover, in some stems, when cut across, the central cylinder soon shrinks down, showing that it is exerting a shortening pull upon the other tissues. I have seen this very marked in *Mamillaria macrothele*.

In several genera, as Opuntia, Rhipsalis, Phyllocactus and Epiphyllum, flat shoots occur, differing somewhat morphologically. These are usually jointed, and the joints commonly represent a year's growth. An important question arises as to how the flattening has been produced, and this has lately been investigated by Vöchting[16] and Goebel.[17] The latter shows clearly that light exercises a direct (not intermediate through natural selection, etc.,) effect in causing the flat form and the growth of the tubercles in Opuntia, and the same probably holds good in other genera. Is it true in others and how widely? The cause of the jointing needs investigation. It is a common xerophilous character as seen in Euphorbias, Kleinia, etc. Is it primarily a growth condition or a characteristic acquired for biological advantage? In some cases at least it is utilized, for joints break off and are rolled away to start in a new place.

It is important to search for other modes of protection in addition to spines. Do any Cactaceæ have a rank odor making them unpalatable to animals? Lewin has recently proven[18] his earlier statement that *Echinocactus (Anhalonium) Lewinii*, a variety of *A. Williamsii*, contains a poisonous alkaloid,[19] and he shows also that four or five others including a Cereus and Mamillaria are likewise provided. But it is not proven that these forms are thereby protected from animals. Are they? And if so, how do animals know that they are poisonous? Is it by smell or sight? They show no warn-

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[16] Pringsheim's Jahrbücher **26**: 483-494. 1894.
[17] Flora **80**: 96-116. 1895.
[18] Ber. der d. b. Gesellschaft **12**: 283. 1894.
[19] See Havard, Bull. Torr. Bot. Club **22**: 117. 1895, where *A. fissuratum* and *E. Lewinii* are said to produce intoxication when chewed.

ing colors, and if animals are not in some way allowed to distinguish the poisonous from the harmless they would destroy the plants before discovering that they are poisonous, and the object of this mode of protection be defeated. Either the animals are warned, or else the presence of the alkaloid is incidental and not an "adaptation" to protection. Not only *E. Williamsii* and closely related forms, but also the species of Anhalonium are without obvious means of protection, unless the hard cuticle of the latter serves to this end. The flattened and roughened and gray colored upper surface of *A. fissuratum* and the fact that they live partly sunken in the earth suggest that they may be protected by their resemblance to the ground on which they grow. Are they? The exudation of nectar already mentioned is perhaps protective, and the arrangement of crystals in a sort of armor just under the epidermis of *Opuntia arborescens* (to be described below) is probably protective against snails. Are any others to be found in the family? A red color occurs on the under surface of Peireskia leaves, on young shoots of Cereus, etc., and on nearly all seedlings. Is this, as Stahl would suggest, associated with the presence of tannin or other distasteful substance, and hence of the nature of a warning color? Or is it in the seedlings a light-screen? The probability of some protection against too great light and heat has already been mentioned, and possibly the hairs, or even the hypoderma may assist in this,[20] but nothing positive is known about it. The investigation of the minimum, optimum, and maximum temperature points for some desert Cactaceæ would give results of great interest. There is reason to think that electrical currents are to be detected on the deserts.[21] Do plants show any relations to them?

The entire relation of form-conditions to climate requires more careful study.[22] Is condensation proportional to dry-

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[20] See McFarlane's suggestion, Bot. Centr. **51**: 184. 1895.

[21] National Geographical Mag. **4**: 171. 1893.

[22] As a basis for such study, the forms se·m to fall into divisions about as follows. Goebel has traced the subject for the genus Opuntia.

a. *The branching, shrubby type*, little removed from the typical condition: the woody Peireskias.

b. *The unjointed column*
- upright
  - ribbed: Cereus, Pilocereus, etc.
  - tubercled: fleshy Peireskias, Cylindropuntiæ.
- creeping or deflexed: creeping Cereus and Echinocereus.

ness of climate?[23] If so, to means or extremes of dryness? It is to be noted that condensation can be more easily effected in the deserts than in cloudier climates, for the great cause in antagonism to condensation, *i. e.*, the need for a large spread of green surface, is here much less operative; for the slow growth of the plants requires less assimilation, and the intense and continuous light render possible a given annual amount of assimilation with a far smaller surface than is possible in cloudier climates. Hence condensation is absolutely easier to desert than other vegetation, and it may mean that the conditions are as not extreme as they appear judged by other standards.

Passing now to internal anatomy, the first great problem is to study it in relation to external conditions. As one views Cactaceæ in collections, he is continually surprised at the apparent lack of relation between the development of the tissues and the supposed habits of the plants. Some forms, such as Rhipsalis, Phyllocactus and some Opuntias, though not very xerophilous in habit (except in some cases where they possess xerophilous characters in common with other epiphytes), possess very strong cuticle, hypoderma and mucilage, while other marked desert forms, such as some Mamillarias, have very slight cuticle and no hypoderma. Even granting that the former cases are examples of survival of old xerophilous characters, how are the latter to be explained? Does tissue anatomy respond sensitively to changing conditions or does it not? Here, perhaps, better than anywhere else, is the opportunity to delimit internal growth conditions from those of "adaptation." A comparative anatomy of the family, studied in relation to life-conditions, and introducing comparisons with the characteristics of other desert families, would be of great value.

The very common collenchymatous hypoderma is proba-

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c. *The jointed column* .. { upright; Cereus testudo. / deflexed: some Rhipsalis species.

d. *Phylloclادia*, two-ribbed flat shoots: Phyllocactus, Rhipsalis, Epiphyllum.

e. *Flattened ribless shoot* { lateral, on cylindric axis: Opuntia Brasiliensis. / all flattened: Platopuntiæ.

f. *Sphere form* (including short columns) { ribbed: Echinopsis, upright Echinocereus, Echinocactus, Astrophytum, Melocactus, etc. / tubercled: Mamillaria, Leuchtenbergia, Pelecyphora, Anhalonium.

[23]Noll has given (Flora **77**: 353-356. 1893) exact data on relation of form to transpiration.

bly water-holding, as is the mucilage, but this is proven in neither case. To the mucilage, Stahl[24] assigns a function of protection against animals, which its abundance in some non-xerophilous forms seem to sustain. The "Nebenzellen" of the stomata are certainly a xerophilous character, but in what way are they? Probably nowhere else in nature, though it is a xerophilous character, are the rings and spirals better developed in tracheids than here—they are particularly superb in Leuchtenbergia, where as elsewhere they often form gland-like masses along or at the ends of fibro-vascular bundles. What is the use of the spirals in this water-holding family? Can it be that the spiral in a tracheid is associated with the *holding* of water, and that it acts by presenting a larger surface and hence stronger capillary attraction for the water? And are the gland-like tracheid masses really water storers, and if so why are they better than the ordinary pith or cortex cells? The entire internal anatomy of Leuchtenbergia is most beautiful and interesting and the study of its development will prove of great interest. Pits between water cells are particularly fine and show thickened plates at the contact-walls. The hairs show many fine markings and are recommended to those interested in the structure of cell-walls. A micro-chemical study of the tissues is needed, for I have frequently found that the reactions to reagents are not such as our suppositions as to the nature of the walls lead us to expect. The crystals are excessively abundant, doubtless in part because of the very slow growth of desert Cactaceæ and the lack of falling parts, leaves and bark. In certain cases, as in *O. arborescens*, use seems to be made of them for they are deposited in a close single layer, apparently as a sort of armor, just under the epidermis, and perhaps hinder the ravages of snails, or other small animals. But do snails occur on the desert and try to eat the Cactaceæ? This is but one of many examples of what seem to be the converting of a disadvantage to use; probably many of the special secretions, substances once purely excretions but converted to protective purposes, are of this origin.

The Cactaceæ show great "vitality," not only in withstanding bad treatment, but in rooting freely from almost any part, as from the leaves in Peireskia, the tubercles in Mamillaria, etc. Perhaps the possibility of free grafting is another phase

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[24] Pflanzen und Schnecken, Jena. 1889.

of it. In what does "vitality" of this sort consist? Is it a more hardy composition of the protoplasm of that plant, or is it in the fact that nearly all cells are alive, i. e., non-skeletal, or a result of the abundant water and food supply in every cell?

The bundle systems are built upon a very uniform system; in the several genera examined they form modifications of that which occurs in Opuntia, which in turn is easily derivable from that of Peireskia. This should be examined for the remaining genera. The bundle systems seem to follow closely external form and morphological changes, a fact which comes out with particular beauty in Mamillaria, where the grooved and ungrooved forms have bundle systems answering exactly to the morphological difference between them. Further study of this relation between internal anatomy and external changes is needed before generalization is possible, but the point is as a principle one of great interest and importance. A careful study of the sieve elements is needed. Many thick forms of Cereus, Melocactus and Mamillaria show a pith-system of interlacing bundles, the development of which is still unknown. In Anhalonium, and confined to it, is found a remarkable bundle-cylinder system. It resembles somewhat, though in more extreme degree, that figured for the separate cylinders of Bauhinia.[25] In cross-section the bundles radiate fan-like in clusters, and then curve about plume-like, so that they often come to face inward towards the center of the stem. Its development is unknown. The entire minute anatomy of this genus, like that of Leuchtenbergia, is of great interest. The composition of the excessively hard cuticle in the rough-tubercled forms, such as *A. fissuratum*, is not known. A latex-system is found in many Mamillariæ (in which the mucilage is generally absent), but its meaning is as little understood here as elsewhere.

The constancy of the behavior of the axillary vegetative points in the same "genus," and the differences in its behavior in different "genera" have suggested that it may be used to indicate true relationships, and I have given in Flora (l. c.) a scheme showing such relationship. This point needs much more full investigation. For systematic purposes, this family needs above all others exact study in the field, for variation is rife in it. The affinities of the family as a whole are not

[25] See Engler & Prantl, Pflanzenfamilien. Leguminosæ, p. 81.

known, different students having placed them in very different positions. If a form is found which will give the transition to some known family, it will probably be a Peireskia-like species growing in the forests of north-western Brazil. All evidence goes to prove the newness of the family, such as their great variability, their lack of sharp divisions between the species and the genera, the large size of some of the latter, the constancy in the structure of the flowers, great similarity in the seedlings, similar characteristics of the axillary vegetative points (differences being derivable by slight modifications in degree), practical confinement in range to a single continent though a very large family, perhaps also their very "vitality," already referred to, including possibility of free grafting and hybridizing.

The study of the development of the flower may give a clue to affinities. Their geographical distribution is imperfectly known. It is worth observing how closely this follows the line of newer mountain chains on the American continent—extending along the Andes and in Brazil to Venezuela through the West Indies to Mexico and northward into the United States.[26]

So much for some of the special questions which, by those who can study the plants in the field or who can command the proper material, should be solvable. In addition to these, certain unusually marked characteristics of the Cactaceæ, in particular their variability, the perfection of their adaptations, and their segregation into many species under a simple environment, make it seem that they are particularly fitted to contribute to the solution of more general problems. As to all of these points, variation, historical development of adaptations, and causes of segregation into species, the old questions remain yet to be answered. Is there or is there not an innate tendency in living matter to variation, or is variation in some unexplained way induced by the surroundings? In the former case, is variation a function of living matter, co-originating with it, or has it been acquired by selection or otherwise, since it gives such good results? In either case, does variation tend of itself to follow certain lines, or is it "fortuitous?" In the former case, are the lines of themselves adaptive or are they adaptive in different directions, natural selection cutting off the unfit and leaving

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[26] See the map in Neumayer, Erdgeschichte, **2**: 655.

the fit? I doubt whether we have as yet any certain knowledge upon any of these points. Inseparably bound up with these questions is that as to the direct effect of the external world. Light makes some shoots grow flat: how much of form and size conditions are thus directly imposed, and hence not due to natural selection? How much to internal constitution or mechanical growth conditions? How much to selective action of the environment? The greatest problem of the present time in the dynamics of evolution, is the delimitation of the effects of these three sets of influences: (1) internal constitution, which includes (*a*) properties or functions of protoplasm, (*b*) hereditary characteristics of the particular organism, (*c*) mechanical, physical or chemical conditions of growth; (2) the direct effect of external, mechanical, physical or chemical influences upon the plastic organism either (*a*) directly, or (*b*) through the intermediation of irritability; (3) the preservation of adaptive variations, and the elimination of the unadaptive by the operation of natural selection. A few years ago an overwhelming preponderance was ascribed to the third, but evidence is accumulating to show that the first and second play a part equally, perhaps more, important. I doubt if any family of plants can equal the Cactaceæ, when properly studied, in their bearing upon these matters.

Aside, however, from this, the family is one which the extreme natural selectionist will find it difficult to deal with. On the deserts the conditions of life are comparatively speaking, very uniform. Heat and light, the gases of the air, the minerals of the soil are more than ample for all, and all share practically alike as to rain. Enemies are not numerous, not highly differentiated, and not of the kind with which they come into competition for survival. The plants grow well apart, and the struggle for existence lacks the complexity of forest and jungle and is reduced simply to a struggle with hard but uniform inorganic nature, the scarcity of water being the greatly preponderating element. Such conditions as these should, upon the natural selection hypothesis, produce a monotonous, little differentiated vegetation, for without keen competition between similar or closely related forms, slight favorable differences have no chance of survival over slight unfavorable ones, and hence differentiation along advantageous lines alone could not occur. Now what are the facts? Despite uniform, non-competitive conditions, this family has produced a thousand species, with some genera including over two hundred species; and in addition has developed hundreds of forms of spines, hundreds of modifications of tubercles and ribs, and hundreds of variations upon other points of its structure. Clearly we must allow for differentiations which are without reference to use. He who believes that differentiation depends solely upon the preservation of favorable over unfavorable variations can find in this family less support for his view than can he who sees in nature the known tendency to variation led along certain lines by little known though omnipresent principles of inertia and segregation, these lines cut off by natural selection when they are opposed to adaptation (*i. e.*, unfit), but allowed when competition is absent to persist whenever not opposed to adaptation (*i. e.*, not unfit, or indifferent) as well as when positively adaptive; until finally when competition comes into play the positively adaptive lines triumph over the indifferently adaptive and natural selection has won the day. I believe the Cactaceæ are in the condition in which there is little competition, and that there are present many indifferently adaptive as well as positively adaptive features of structure, and that the former sometimes are not much behind the latter in degree of differentiation.

Smith College, Northampton, Mass.